Oceanic processes and the recruitment of tropical fish at Rottnest Island (Western Australia)

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Abstract

Transport processes relating to the observed annual "pulse" of tropical fish larvae arriving at Rottnest Island each autumn are examined using historical current measurements in the Leeuwin Current near the Abrolhos Islands and along the continental shelf just north of Perth. Observations of two common damselfish between 1977 and 2002 (with enhanced detail of fish size categories from 1994) show that the bulk of new recruits settle at Pocillopora Reef in March/April, a time when the Leeuwin Current is strengthening and the Capes Current is waning. Very large recruitment pulses in 1999 and 2000 were in *La Nina* years when the Leeuwin Current was very strong and water temperatures were at record high levels, but a third relatively strong pulse in 1995 was during an *El Nino* period with a weak Leeuwin Current (albeit with elevated ocean temperatures). Both advection and temperature therefore appear to play significant roles in recruitment at Rottnest Island, while biological factors such as food and predation during the pelagic stage must also be considered. The potential role of algal rafts in enhancing larval transport and survival may be important in the recruitment process and needs further research.

Keywords: Leeuwin Current, oceanic processes, larval transport, fish recruitment

Introduction

Many, if not most, marine fish species undergo a pelagic larval migration phase as part of their life cycle. This process serves to disperse the larvae away from the spawning area, leading to potential recruitment/colonisation at distant locations (depending on the duration of the pelagic phase) where they settle and complete their life cycle.

Ocean currents accordingly play a major role in the dispersal process, and off Western Australia the Leeuwin Current is the dominant boundary current, flowing southward down the Western Australian coast and then eastwards along the south coast (Cresswell & Golding 1980).

The existence of a warm offshore current had been postulated as early as the 1890's by Saville-Kent (1897) to explain the presence of tropical species at the Abrolhos Islands. The progressive southwards shift from tropical to temperate fauna was identified by Michaelsen (1908), who surveyed the nearshore waters from Shark Bay to Albany in 1905, and he too felt that a warm southward current must be responsible for the presence of *Pocillopora* corals as far south as Rottnest Island. Hodgkin *et al.* (1959) recognised the distinction between the "Flindersian" (warm temperate) marine species along the mainland coast and on some sections of Rottnest Island against the more "Damperian" (tropical) species found dominantly on the western end of the Island. Likewise, the increased abundance of tropical molluscs on the western end of the Island compared with the eastern coast was attributed to the newly-discovered Leeuwin Current by Wells (1985).

Rottnest Island lies some 18 km west of Fremantle (Figure 1) near the edge of the continental shelf and is frequently bathed by Leeuwin Current waters either directly (when the Current is flowing along the outer shelf) or indirectly (by cross-shelf processes when tongues of warm Leeuwin Current water penetrate shorewards – Pearce *et al.* 2006a). Clearly, the Island is in an interesting overlap zone where both tropical and temperate marine species are encountered, partly as a result of the Leeuwin Current which acts both as a conduit for the southward transport of tropical fauna and also maintains relatively high temperatures around the Island.

Exploratory surveys of the reef fish distribution along the Western Australian coast (Hutchins 1977, 1994, 1997a) confirmed a progressive change from dominantly tropical species in the north to a largely warm-temperate component in the south. Tropical forms were found to make up 64% of the species at the Abrolhos Islands (29°S – Figure 1) while at Rottnest Island only 30% of the species were of tropical origin and 53% warm-temperate (Hutchins 1994), and there was also a marked reduction

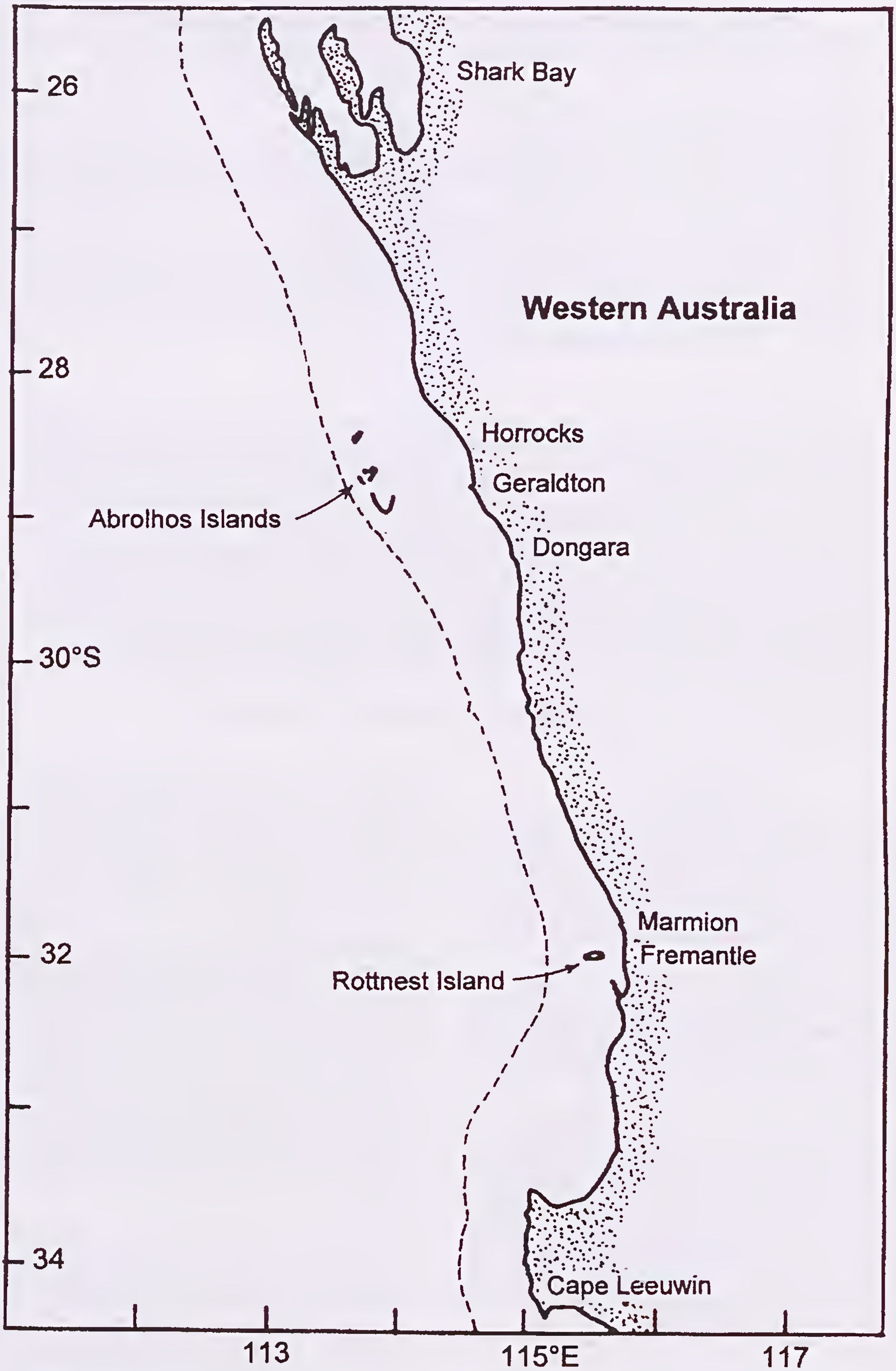

Figure 1. Location chart showing the main sites mentioned in the text. The dashed line marks the edge of the continental shelf.

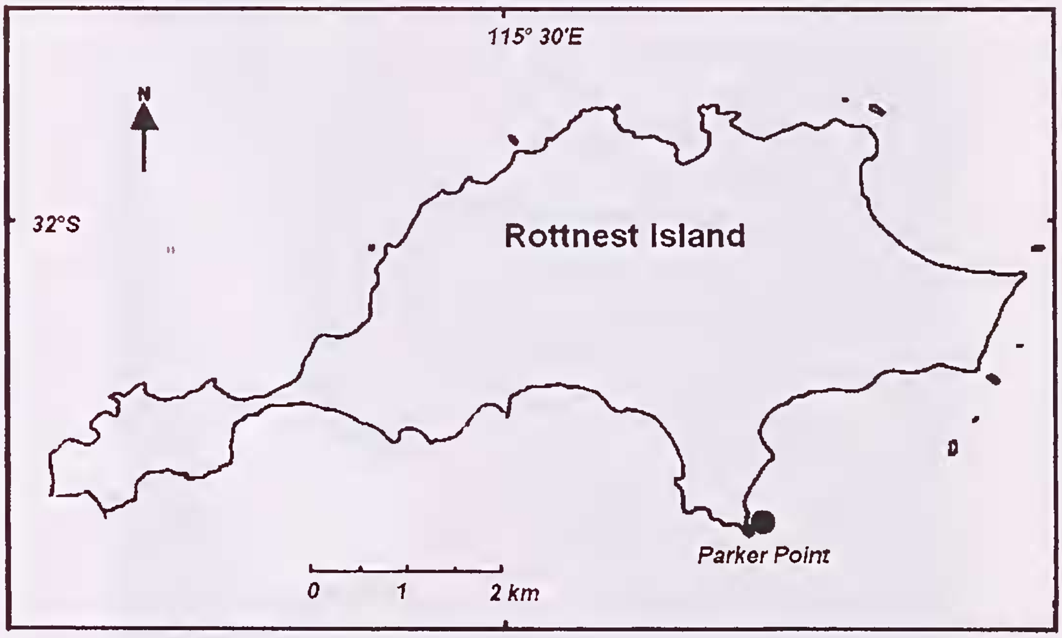

Figure 2. Location chart of Rottnest Island showing the observation site at Parker Point.

in tropical species between these offshore islands and the adjacent mainland coastal waters at the same latitude (Hutchins 1994). In a more recent study, Watson & Harvey (2009) found tropical species made up 66% of the fish fauna at the Abrolhos compared with only 2% at Rottnest Island.

Observations of tropical fish in the shallow bays around Rottnest Island over the past 25 years have revealed the annual arrival of larval recruits each autumn. Hutchins (1991) found that the tropical fish fauna tend to concentrate along the southern coasts of the Island, and in particular in the area near Pocillopora Reef off Parker Point (Figure 2). Here, there is a conspicuous reef of the coral species *Pocillopora damicornis* which attracts newly arrived recruits and also supports longer-term populations of tropical (and other) fish. An influx of very small juvenile fish commences in autumn and continues spasmodically until as late as November in some years (Hutchins 1991), but there are large inter-annual differences in settlement numbers.

Two common damselfish (*Abudefduf sexfasciatus* and *A. vaigiensis*) are among the most visible and abundant recruits at Parker Point. These 2 species have been found on reef systems from the Dampier Archipelago (21 °S – Hutchins 2003), at Ningaloo Reef (22 °S – Hutchins 1994), Shark Bay (25 °S), and offshore at the Houtman Abrolhos Islands (29 °S: Hutchins 1994; Hutchins 1997b). Rottnest Island appears to be their southernmost habitat along the Western Australian coast, based both on the published literature and by personal observation by Hutchins (hereafter denoted BH). While Hutchins (1997a, 1997b) has observed breeding behaviour at the Abrolhos Islands, no breeding activity has been observed at Rottnest Island (BH) and so there is presumably no local recruitment of these 2 species at the Island.

A survey of larval fish along a transect some 50 km north of Rottnest Island (Muhling & Beckley 2007; Muhling *et al.* 2008; Beckley *et al.* 2009) found that the temporal and spatial structure of larval fish assemblages was closely linked with the seasonally-varying current system and water mass structure across the shelf. During this study, three *Abudefduf* larvae (species not documented) between 2.6 and 3.3 mm in length were caught at mid-shelf in water depths of about 40 m in early April 2004 (Muhling 2006; pers.comm.), which coincides with the timing of new recruits at Rottnest Island.

This paper presents the observations of larvae and juveniles of the two *Abudefduf* species at Parker Point in relation to oceanographic processes off south-western Australia. Three stages of the life cycle (dispersal, alongshore transport, and settlement) are examined in some detail. In particular, mechanisms of larval transport are explored using existing knowledge of the Leeuwin Current and the flow on the continental shelf, and a simple web-accessed trajectory model (Aus-Connie: Condie *et al.* 2005) is used to assess connectivity between the Abrolhos Islands and Rottnest Island.

The current system along the Western Australian coast

Because of the importance of the alongshore and cross-shelf advection processes in the dispersal of marine larvae, we briefly review the seasonality and main characteristics of the current systems off Western Australia. Small-scale, more localised circulation patterns near the Abrolhos and Rottnest Islands are dealt with in the Discussion.

Sea-surface temperature images from the Advanced Very High Resolution Radiometer (AVHRR)) on the NOAA satellites show the Leeuwin Current flowing strongly southwards as a jet along the shelf break and outer shelf during the winter/spring months, often with mesoscale meanders/eddies sporadically carrying the

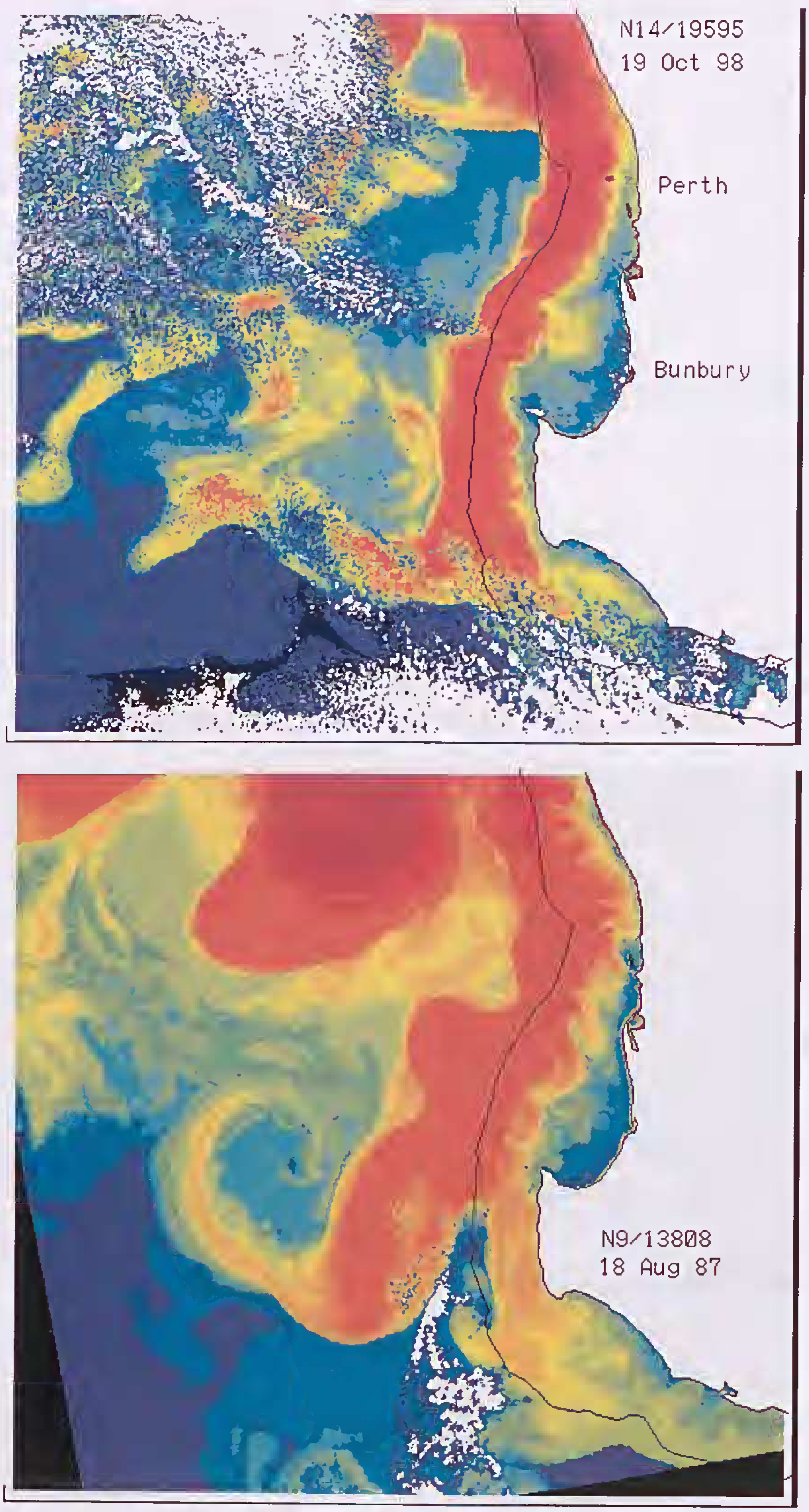

Figure 3a & b. Sea-surface temperature (SST) satellite images from the Advanced Very High Resolution Radiometer (AVHRR) on the NOAA series of satellites in (upper panel) October 1998 and (lower panel) August 1987. The brightness temperatures in AVHRR Band 4 are shown (not corrected for atmospheric effects). The temperature colours are different in each image because they have been enhanced to illustrate the desired features of the flow patterns; they vary from the warmest water (in red/orange) through yellow/green to the coolest water in blue. Images by courtesy of CSIRO Marine and Atmospheric Research and the Western Australian Satellite Technology and Applications Consortium (WASTAC).

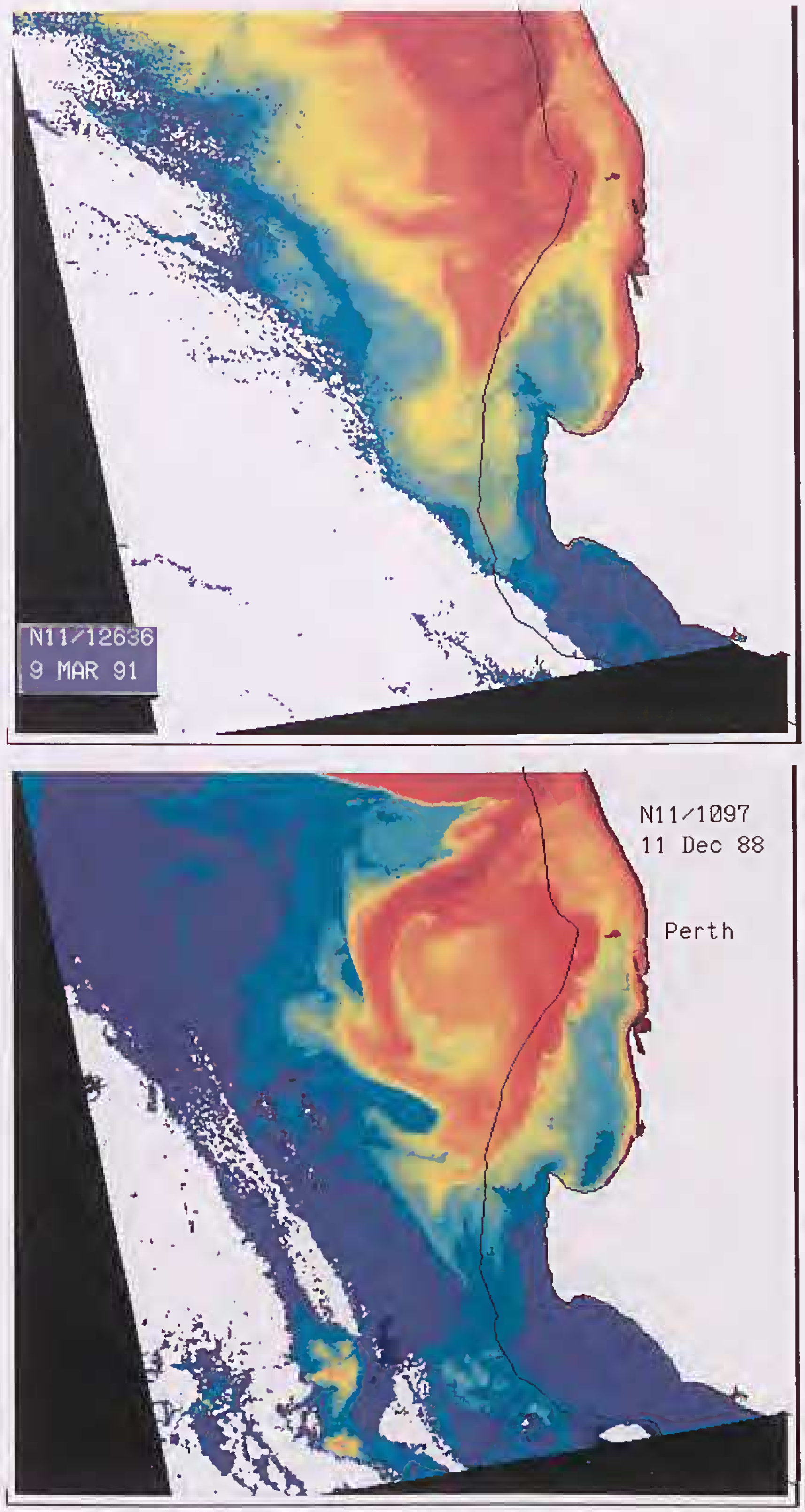

Figure 3c & d. As for Figure 3a & b, but for (upper panel) March 1991 and (lower panel) December 1988.

warm waters offshore in large (~ 200 km) loops (Figures 3a,b). In summer, the Leeuwin Current weakens in response to the strong southerly (northward) wind forcing and the coastal Capes Current can be seen pushing cooler water northward along the inner and mid-shelf (Pearce & Pattiaratchi 1999; Gersbach *et al.* 1999; Figure 3c). On occasion, the large eddies can temporarily distort the normal southwards flow of the Leeuwin Current – note the 150 km diameter anticlockwise eddy between Perth and Cape Naturaliste in Figure 3d, causing northward flow along the shelf-break past Rottnest Island.

On a more local scale, smaller (~ 10 to 20 km) tongues of Leeuwin Current water are evident penetrating shorewards across the continental shelf (*e.g.*, Figure 3b), indicating an active mechanism for the cross-shelf exchange of water and hence planktonic larvae. In addition, Figures 6 and 8 in Pearce *et al.* (2006a) show that bands of warm Leeuwin Current water can curl in towards Rottnest Island from the north and also wrap around the southern shore on occasion, thus providing a mechanism contributing directly to recruitment at the Island itself.

There have been few moored current measurements in the Leeuwin Current. During the 1986/87 Leeuwin Current Interdisciplinary Experiment (LUCIE: Smith *et al.* 1991; Church *et al.* 1989) current moorings off Dongara (Figure 1) showed the Leeuwin Current flowing persistently southward between February and June 1987, with near-surface speeds of 50 cm/s to 1 m/s (Boland *et al.* 1988). At other times, there were bursts of southward flow at similar speeds punctuated by brief and much weaker northward current reversals. Feng *et al.* (2003) have shown that the Leeuwin Current transport is greatest in winter but the mean surface current peaks in April.

Currents along the continental shelf exhibit a strong seasonal pattern which is largely driven by local wind forcing. During the summer months, the Capes Current (Pearce & Pattiaratchi 1999; Gersbach *et al.* 1989) flows northward at 5–15 cm/s (Steedman & Associates 1981; Cresswell *et al.* 1989; Pattiaratchi *et al.* 1995; Pearce *et al.* 2006a) although speeds of 30 cm/s can be experienced under strong southerly wind conditions. In winter, on the other hand, the currents are largely southwards with speeds of between 5 and 20 cm/s (Steedman & Associates 1981; Cresswell *et al.* 1989; Pattiaratchi *et al.* 1995; Pearce *et al.* 2006a). In all seasons, current reversals and shorter-term pulses of current of up to 50 cm/s (1 knot) can occur.

Data sources and processing

Oceanography/meteorology

Because of the established link between the Leeuwin Current and El Nino/Southern Oscillation (ENSO) events (Pearce & Phillips 1988), monthly values of the Southern Oscillation Index (SOI – an indicator of the intensity and duration of ENSO phenomena, based on the difference in atmospheric pressure between Tahiti and Darwin) were obtained from the website http://www.bom.gov.au/climate/current/soihtm1.shtml (verified August 2007).

Coastal sea level can be used as an index of the "strength" of the Leeuwin Current (Pearce & Phillips 1988; Feng *et al.* 2003), so monthly sea level data for Fremantle were acquired from the National Tidal Centre in Adelaide. Monthly anomalies were derived by subtracting the overall mean seasonal cycle from the individual monthly sea levels, and 3-month moving averages were taken to smooth smaller-scale variability and emphasise the dominant ENSO-related fluctuations.

Monthly sea surface temperatures (SST) were obtained on a 1-degree latitude/longitude grid (approximately 100 km) from the Reynolds global dataset (Reynolds & Smith 1994). The selected grid was for the area 31° to 32°S, 115°E to the coast, generally reflecting open-ocean conditions immediately northwest of the island and hence including the Leeuwin Current. Monthly anomalies were derived and smoothed as for sea levels. Local water temperatures at Parker Point were taken from satellite-derived measurements between 1995 and 2001 by Pearce *et al.* (2006b), while the nearshore temperature cycle at the adjacent mainland coast was derived from temperature loggers off Marmion between 1990 and 1994 (Figure 1; Pearce *et al.* 1999).

Fish surveys

Visual surveys of the fish fauna in the nearshore waters of Rottnest Island were undertaken between 1977 and 2002. While observations were made in a number of bays along the southern and western coasts of the Island (Hutchins & Pearce 1994), it was found that the bulk of the recruitment occurred off Parker Point (Figure 2) and so most of the effort from 1994 focussed on Pocillopora Reef in Parker Point Marine Reserve. The water depth over the reef was 1 to 2 m, with some areas being exposed at low spring tides.

During each survey, a diver (BH) swam a grid pattern lasting about an hour along a transect which followed the extensive system of *Pocillopora* colonies and ended in the rocky shallows near the Parker Point headland. The survey route was always the same, giving a good coverage of the reefs in the study area, and was planned so that the chances of counting a fish twice was unlikely. 20 fish species were identified and counted (Hutchins & Pearce 1994), but in our analysis here only the damselfishes *Abudefduf sexfasciatus* (Scissortail Sergeant) and *A. vaigiensis* (Indo-Pacific Sergeant) were used as they were readily identifiable and they also remained in the open after settling (unlike those fish that tended to hide after settlement – Hutchins 1991; Hutchins & Pearce 1994). These tropical reef-dwelling fish are not endemic to Western Australia (Hutchins 1994) but are widely distributed in the Indo-Pacific region. Choat (1991) has classed them as omnivores, feeding largely on zooplankton and benthic algae. They have been recorded as both juveniles and adults at Rottnest Island but not at the adjacent mainland coast (Hutchins 1991). The Scissortail Sergeant can grow to a length of some 16 to 22 cm (Allen & Swainston 1988; www.fishbase.org; www.amonline.net.au/FISHES/fishfacts/fish/asexfasc.htm), while the Indo-Pacific Sergeant reaches a maximum length of 20 to 22 cm (Allen & Swainston 1988; www.fishbase.org; www.amonline.net.au/FISHES/fishfacts/fish/avaigiensis.htm).

In the earlier years from 1977, visual counts were made of the total numbers of selected species observed and the first observation of new recruits noted, but since 1994 the various stages of growth were visually classified into 6 categories, ranging from just after arrival (when they still retained their planktonic morphology) up to the sub-adult stage, are shown below:

Class/description	Standard Length SL mm	Total Length TL mm
a = minute juvenile with pelagic colouration/features	11–17	15–23
b = very small juvenile	19–26	25–36
c = small juvenile	30–40	40–55
d = juvenile	45–57	65–77
e = large juvenile	60–72	80–100
f = sub-adult (i.e., about to mature)	75 +	110 +

The change from one category to the next was somewhat subjective. The estimates for the Standard Length (SL, which does not include the tail) and the Total Length TL (including the tail) were based on measurements of a selection of the sampled fish. As *Abudefduf sexfasciatus* and *A. vaigiensis* have similar maximum lengths and there do not seem to be any obvious size differences in the early growth stages, we believe these categories are adequate for both species. Category "a" is the pelagic larval phase of the life cycle and "b" represents the first post-settlement juvenile stage, these 2 phases being the main focus of this paper. The smallest and largest individuals in the pelagic category "a" observed at Rottnest Island were about 17 mm and 23 mm TL respectively; the 15 mm TL fish (estimated age of about two weeks) was collected from floating *Sargassum* to the north of Rottnest. Most new recruits of the two *Abudefduf* species arriving at Rottnest had a transparent silvery colour, but they quickly developed dark bars on the body after settling. However, those that had spent some time under rafts of floating *Sargassum* could arrive at the island with the full juvenile colouration. Larvae that survived from the commencement of settlement in March or April usually reached the sub-adult stage by the end of the year. As no breeding activity was ever observed during any of the surveys at Rottnest Island (BH), we believe there was no recruitment from local populations and all new recruits must therefore have arrived from a northern source.

It was found that *Abudefduf* recruitment always occurred in the same locations (shallow areas with good protection from wave action) and the larvae preferred to settle in reef areas just below the water's surface: small juveniles were rarely found on reefs with depths of more than 1 m (at high water). The first recruits always arrived in the shallow protected reefs behind Parker Point headland and in many years that was the only location where recruits were found. The more exposed reefs in the study area only received recruits during periods of heavy settlement (such as 1995, 1999 and 2000 – see Results below), suggesting that the more favourable areas had become overcrowded. It appears therefore that the more exposed areas were less favourable to recruitment as in low settlement years new recruits were rarely found there, and certainly these areas had the greatest mortality during winter storms. The larger juveniles tended to move from their initial settlement sites in the reefs behind the headland to more exposed areas closer to the edge of the lagoon to feed as the flow of water (and presumably plankton) into the lagoon was greater there.

The number of sampling days at Parker Point was somewhat sporadic (Table 1), especially the period 1986

Table 1

Number of fish surveys per month at Parker Point Marine Reserve. Bolded-underlined entries are the months when new recruits were first sighted.

Year	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
1977			2						1			1
1978				**1**		1	1	1	1	2		1
1979	1		1		**2**		1	1				1
1980			**2**	1	1	1		1		1		
1981								1				1
1982				**2**		1	1			1		
1983	2	1	1	**1**	1	1	1		1	1	2	1
1984	1		2	**1**	1	2	1	1	1	1	1	2
1985	1	1	**2**		2	1	1		1	1		1
1986												
1987												
1988									1			
1989			1								1	
1990				1								2
1991			1	**3**	1			1			1	
1992	1	1	1	**2**	1	1	1	1		1	1	
1993	1			1	**1**		1	1		1	1	
1994			1	**4**	2	3		1	1	1	1	1
1995	2	1	**2**	1	1	2	1	1	1	2	1	1
1996	1	**1**	1	1	1	1		1		1	1	1
1997	1	1	**1**	1	2	2	1	1	1		1	
1998	1	1	1	**1**	2	1	2	1	1	1	1	1
1999	1	1	**4**	2	2	1	3	1	1	1	2	1
2000	**1**	2	1	2	1	2		1	1	1	2	1
2001	1	1	**2**	4	1	2	1	2		2	2	
2002	1	1	**2**		2				1		2	
2003				1								
Totals	16	12	28	30	24	22	16	17	13	18	20	16

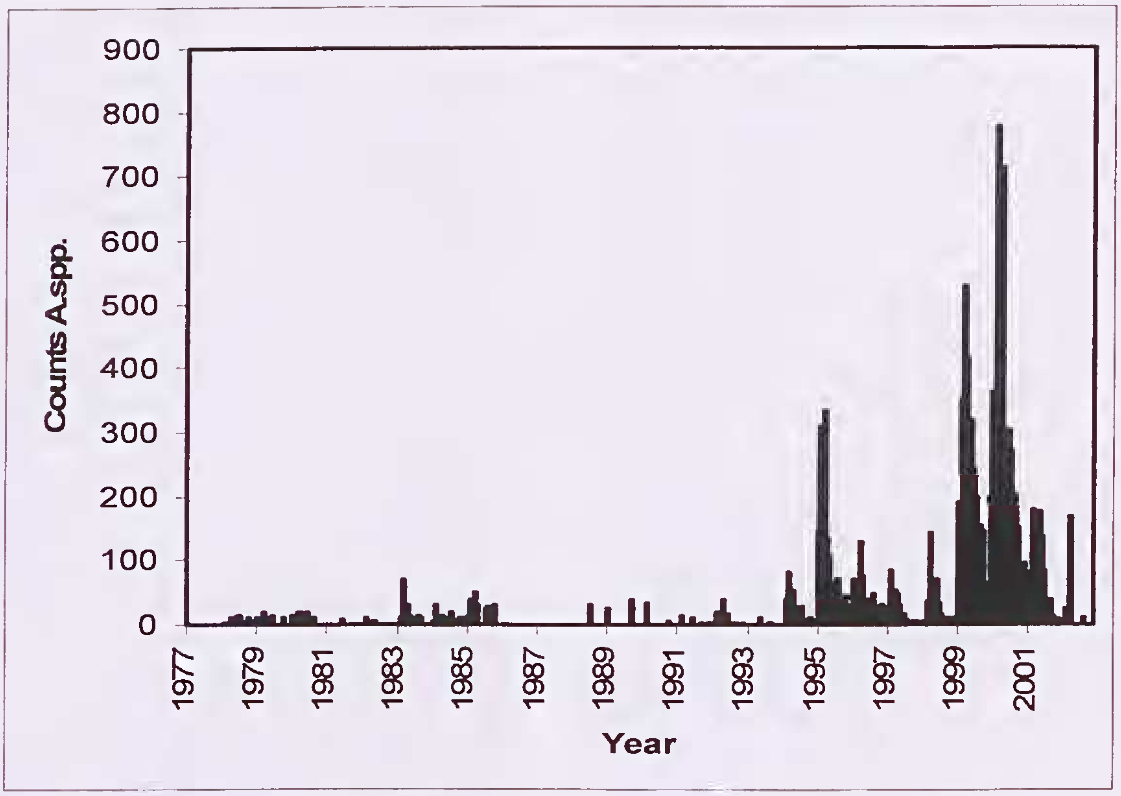

Figure 4. Numbers of all size classes of the two *Abudefduf* species (combined) at Parker Point from 1977 to 2002.

to 1990, due to diver availability, weather conditions, *etc.*, a total of 232 days of observations were undertaken.

Because of the irregular nature of the sampling, short-term (*e.g.*, daily) variability in larval abundance is not known but we believe that the observed larval and juvenile counts realistically reflect the general monthly abundance of the fish – this is borne out by the extended period (weeks to months) of the larval peaks shown below in Figure 5. These peaks in recruitment of the two *Abudefduf* species at Parker Point were matched by the arrival of large numbers of other tropical fish larvae both at that site and many other sites around the Island (BH personal observations); *Abudefdufs* were nearly always the first arrivals at any site. The most noticeable short-

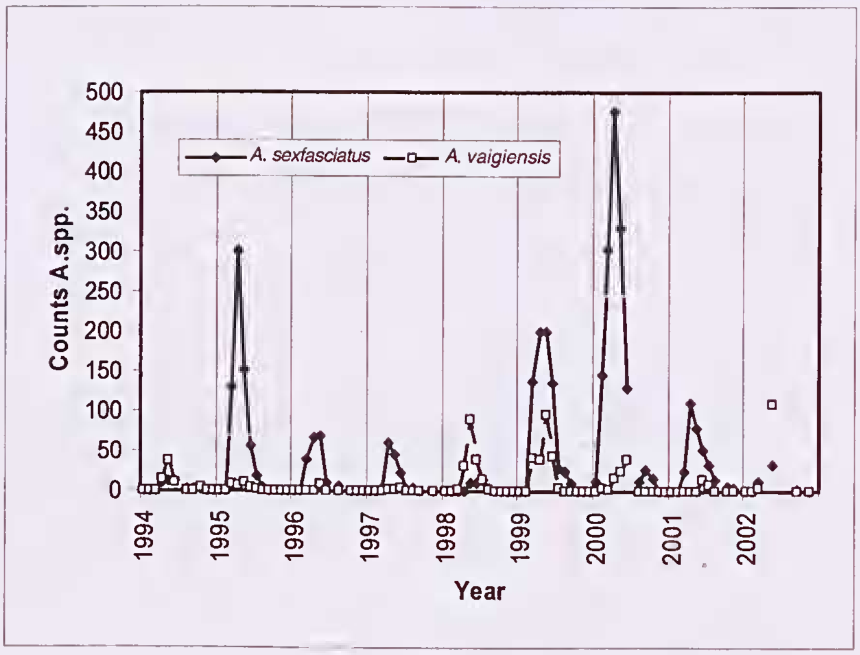

Figure 5. Numbers of category "a" and "b" larvae of the two *Abudefduf* species for the enhanced observational period 1994 to 2002, signifying the arrival of new recruits. Note that many of the monthly counts were very low (often <10 – see Figure 6) and are therefore indistinguishable from zero on this scale. Missing observations have been left blank.

term changes occurred after winter storms when numbers were always considerably reduced.

A consistent monthly time-series was derived by taking the maximum number of category "a" and "b" fish observed during all surveys in each month to facilitate further analysis against the monthly environmental data.

Results

Larval fish abundance at Parker Point

Abudefduf numbers at Parker Point were highly variable since the observations commenced in 1977. The fish were found there throughout the year (Figure 4), but two features dominated: a dramatic rise in numbers from 1995 onwards, and three major peaks of progressively increasing abundance in 1995, 1999 and 2000. Although the surveys effectively ended in 2002, anecdotal information from other observers indicated that these high recruitment levels have not been repeated since 2000. It is planned that regular observations will recommence during 2009 (BH).

The enhanced observations after 1994, which distinguished between the two *Abudefduf* species and also separated out the various size classes, showed that juveniles of *A. sexfasciatus* generally outnumbered *A. vaigiensis* and were by far the main contributors to the recruitment peaks (Figure 5). *A. vaigiensis* really only contributed materially to the 1999 peak, and small pulses of *vaigiensis* in 1994 and 1998 were not matched by *sexfasciatus*. The largest classes were assumed to be survivors from the previous year's recruitment based on their growth over the intervening year. These sub-adults and adults were observed to be very mobile, moving from reef to reef, and so could be difficult to locate from one survey to the next; as a result, the abundance of the later stages could vary tremendously between surveys and may have had little to do with survivorship.

Recruitment of category "a" and "b" juveniles clearly peaked between March and June, tailing off through winter and into spring (Figure 6). The monthly mean abundance (Figure 7c) shows that *A. sexfasciatus* tended to reach peak abundance earlier (March/April) than *A. vaigiensis* (May), although in 1998 the first *sexfasciatus* recruits were not spotted until July. Dramatic losses of fish could occur during the winter and spring months, such as between late June and mid-August 2000 when over 400 individuals disappeared in the northern reefs, probably as a result of storms.

The months when the first category "a" larvae of *A. sexfasciatus* and *A. vaigiensis* were observed in each year (when there were sufficient autumn observations) were:

Month	**Year**
January	2000
February	1996
March	1980, 1985, 1995, 1997, 1999, 2001, 2002
April	1978, 1982, 1983, 1984, 1991, 1992, 1994, 1998
May	1979, 1993

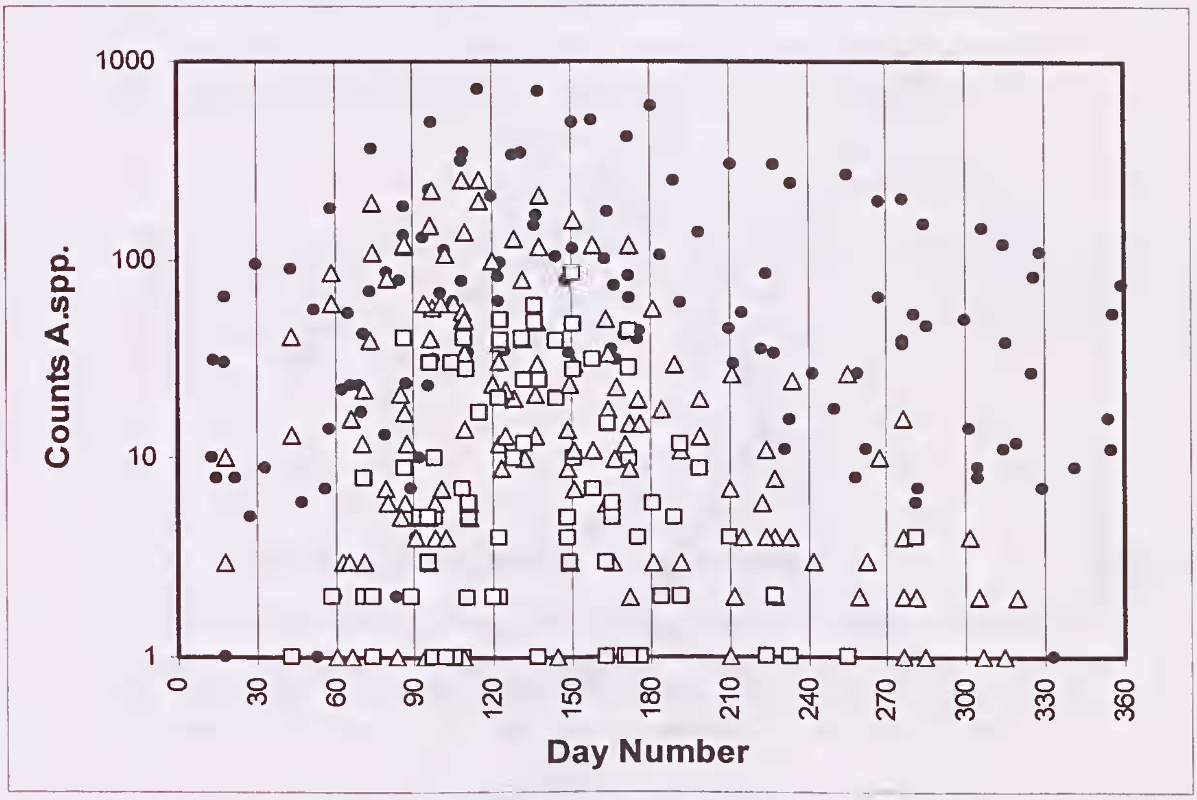

Figure 6. Numbers of the two *Abudefduf* species at Parker Point for the period 1994 to 2002 collapsed into a single calendar year (for plotting convenience divided into 30-day months). Small dots are the total counts (all size classes), while the larger open symbols are for category "a" and "b" larvae only: *A.sexfasciatus* triangles, *A.vaigiensis* squares. Note the log scale.

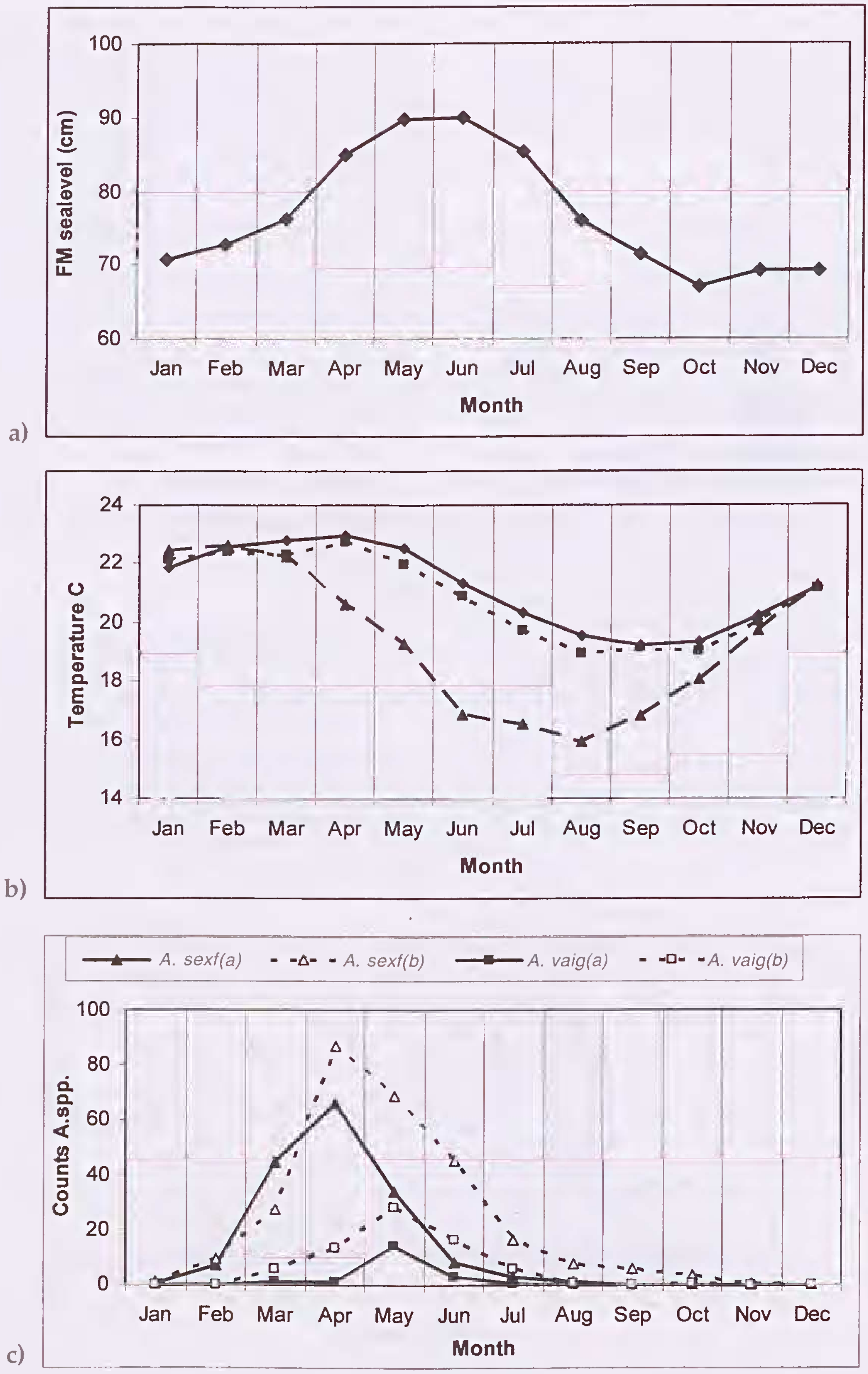

Figure 7. Annual cycles of (a) Fremantle sea level (representing the strength of the Leeuwin Current); (b) water temperature in the 1-degree square north of Rottnest Island (diamonds), at Parker Point (squares) and at Marmion (triangles); and (c) the abundance of categories "a" and "b" of *Abudefduf sexfasciatus* and *A.vaigiensis*.

Oceanography

Monthly mean values of Fremantle sea level (an index of the strength of the Leeuwin Current – Pearce & Phillips 1988) and water temperatures along the south-western Australian coast reflect both the influence of the Leeuwin Current offshore and the annual heat flux cycle in nearshore waters – Pearce *et al.* (2006a). The arrival of new tropical fish recruits at Rottnest Island (Figure 7c) coincided with the seasonal strengthening of the Leeuwin Current in March/April/May (Figure 7a) maintaining relatively high monthly-averaged temperatures of about 23 °C along the outer shelf, including Rottnest Island, well into May (Figure 7b). On average, the temperature dropped to 19 °C in September – an annual range of only 3 °C. By contrast, the nearshore water temperature peaks at 22.5 °C in February and then cools as a result of heat loss to the atmosphere, so by August the monthly average temperatures are down to about 16 °C (Pearce *et al.* 1999), representing a mean annual range of 6.5 °C. Individual temperatures can be as low as 13 °C during the winter months (ibid.), almost certainly too low for survival of tropical fish (BH).

At inter-annual scales, previous studies (*e.g.*, Pearce & Phillips 1988) have demonstrated that there is a generally close relationship between the monthly Southern Oscillation Index (SOI), Fremantle sea level (FMSL) and sea surface temperature (SST). Over the 26-year period 1977 to 2002, the correlation between the SOI and FMSL anomaly was 0.719 (312 observations), while that between the FMSL and SST anomalies (252 months from 1982 to 2002) was also 0.719 – these are both highly significant at the 99% level (Snedecor & Cochran 1980). During ENSO periods with a low SOI, sea levels were low (implying a weak Leeuwin Current – Feng *et al.* 2003) and the sea surface temperatures were correspondingly lower than average, while *La Ninas* were associated with high sea levels (stronger Leeuwin Current) and warmer water.

As seen in Figure 8, the period of enhanced fish observations from 1994 was preceded by an extended ENSO event (or series of events), and there was also an intense episode in 1997/1998 and a weaker one in 2002/2003. 1996 and 1999/2000 were both very strong *La Nina* periods with high sea levels and record high temperatures. There was an anomalous period in 1994/early 1995 when sea level and SST were opposed: the water was comparatively warm even though the Leeuwin Current was weak (low sea level), and there was also a similar but less pronounced event in late 1997.

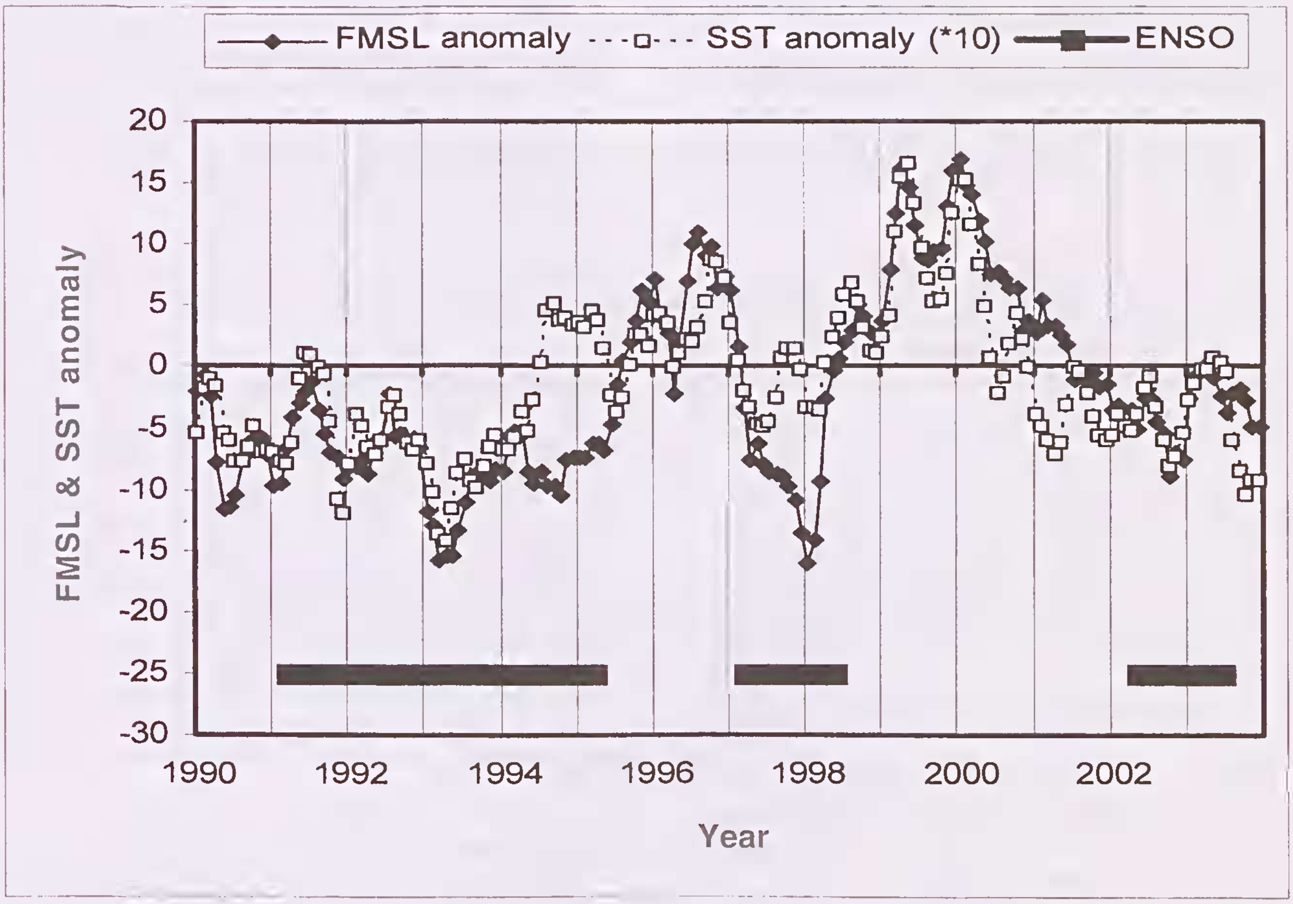

Figure 8. Monthly values of Fremantle sea level anomaly FMSL (see text) and the Reynolds sea-surface temperature anomaly SST (scaled by a factor of 10) from 1990 to 2003. A 3-month moving average filter has been applied to reduce small-scale variability. The solid bars represent ENSO periods.

Discussion

The duration of the pelagic phase is obviously crucial to the distance the larvae can travel before settling. Wellington & Victor (1989) used otolith daily growth increments to estimate the pelagic larval duration of *A. sexfasciatus* as 17.3 days (range 16 to 18 days) and 18.3 days (17 to 20) for *A. vaigiensis*. These are slightly shorter than Thresher *et al.'s* (1989) estimates of 19 to 27 days for *vaigiensis*, but a number of environmental factors can alter the larval growth and duration (Bergenius *et al.* 2005) so we will use 20 days in this paper.

Although many biological and oceanographic processes will play a role in successful recruitment of larval fish, we here focus on the role of the current system on the transport of *Abudefduf* larvae to Rottnest Island. To this end, three distinct stages of the life cycle are examined:

a) hatching and dispersal from the Abrolhos Islands;

b) southward transport in the Leeuwin Current and/or continental shelf currents;

c) settlement and recruitment at Rottnest Island.

The historical current measurements presented earlier are used to quantify the alongshore advective phase (b); while they were not co-incident with the significant larval settlement events found at Rottnest, they are used to provide an estimate of the likely transport rates of the larvae. In applying these results, we will use the convenient "rule-of-thumb" that 1 cm/s ~ 1 km/day – this is accurate to about 15%.

There is little information on the specific life histories of *Abudefduf sexfasciatus* and *A. vaigiensis* in the literature, so we have made use of whatever published information is available on damselfishes generally together with BH's local observations.

a) Dispersal from the Abrolhos Islands

Hutchins (1997a) defined a breeding population as one with a reasonable number of individuals representing most size classes. He found breeding populations of the two *Abudefduf* species at Shark Bay during a survey in May 1995 and at the Abrolhos Islands in February and May 1994, but no evidence of breeding at Rottnest Island. Nest-guarding behaviour was very evident at the Abrolhos Islands during the February survey (BH) and probably contributed to some local recruitment. Nevertheless, Hutchins (1997a) has suggested that the Abrolhos populations may also be maintained by transport via the Leeuwin Current from source regions further north such as Shark Bay (25°S) and perhaps even Ningaloo (22°S).

Hutchins' (1994) surveys at the Abrolhos Islands were centred on the Wallabi and Easter groups; *Abudefduf sexfasciatus* is listed as one of the 10 most abundant species there. The most diverse fish faunas were found on relatively sheltered reefs bordering the passages between the island groups and hence subject to the currents flowing between the islands.

As early stage *Abudefduf* larvae can be found off Rottnest Island for much of the year (Figure 6), spawning at the Abrolhos must also be spread over the seasons. However, the major pulse of new recruits arriving at Rottnest in March/April of most years suggests that a major spawning event may occur at the Abrolhos in February/March and that both environmental factors and food/predation must be particularly favourable for survival at this time of year.

The eggs are laid in patches on reef substrate and embryonic development occurs over 3 to 6 days (Wellington & Victor 1989). The eggs are buoyant and when they break free from the reef they rise into the water column; after a few days the larvae hatch and undergo the pelagic migration phase (see (b) below). These early larvae have limited swimming ability and are therefore largely planktonic, being at the mercy of ocean currents for dispersal away from the Islands.

Cross-shelf currents of 5 to 10 cm/s (Cresswell *et al.* 1989; Pearce & Phillips 1994) could move the larvae either offshore into the Leeuwin Current or shorewards into the seasonally-reversing current system on the continental shelf. Because, however, the summer wind regime at the Abrolhos Islands is strongly from the south (with a diurnally-varying sea breeze component – Pearce 1997; Gaughan & Mitchell 2000) resulting in a net offshore Ekman drift of the near-surface waters, it is in fact most likely that the larvae are carried offshore into the Leeuwin Current regime.

Larvae have been observed using floating objects and *Sargassum* rafts (Dempster & Kingsford 2004) both as a shelter and a source of food. Both larval and juvenile *Abudefduf saxatilis*, for example, have been observed under Sargassum weed in the North Atlantic Ocean (South Atlantic Fishery Management Council 2002). Hutchins (1994) reported that large areas around the Abrolhos Islands are covered with macroalgae, so any detached floating algal masses would also follow the wind-driven transport, possibly "collecting" larvae *en route* and hence assisting the dispersal process.

Water temperature can play an important role in all phases of the life cycle of fish, including their development, growth, swimming ability, reproductive performance and behaviour, and it is the early larval stages that are most sensitive to temperature changes (Munday *et al.* 2007). Warmer waters result in shorter incubation periods, increased growth rates, shorter planktonic durations and higher swimming abilities (*ibid.*). The annual mean temperature cycle at Rat Island in the Houtman Abrolhos group ranges from a summer peak of 23.7 °C in March down to 20 °C in August/September (Pearce 1997), so the presumed *Abudefduf* breeding and dispersal period is effectively at the time of peak temperature. It is worth noting that nearshore temperatures at Dongara on the adjacent mainland coast (Figure 1) peak at 24 °C in January/February and drop to 17.5 °C in July/August (Pearce *et al.* 1999), substantially cooler than those at the offshore islands during the winter months (as originally observed by Saville-Kent 1897).

b) Alongshore transport by the current system

The alongshore transport of fish larvae must be accomplished by the Leeuwin Current and/or the seasonally-reversing current system on the continental shelf. Although the mid- to later-stage larvae have a strong swimming ability, we will view them as passive drifters until they are within striking range of Rottnest Island when their swimming ability becomes important (section (c) below).

As shown earlier, the Leeuwin Current transports tropical waters southwards along the outer continental shelf and upper slope, most strongly during late autumn to early spring. Historical current measurements, however, indicate that the currents can be highly variable between months and years and do not always follow the traditional seasonal pattern. Southward current speeds in the Leeuwin Current itself can average between 40 and 60 cm/s over a month during the period of highest flow rate, with peak short-term speeds of double that. Any larvae which become entrained into the offshore eddy field (*e.g.*, Figure 3) are unlikely to return to the coast within the 3 week larval period and will probably perish, although under favourable circumstances those that are ejected near the shelf-break may survive to cross the shelf and settle at the Island (Holliday pers.comm.).

Mean current speeds on the continental shelf are more like 5 to 20 cm/s with a pronounced seasonal change between southwards flow in winter and a fairly consistent northward tendency (the Capes Current) in summer, with high levels of variability in both speed and direction in all seasons. Larvae originating at the Abrolhos Islands in February/March would probably encounter the Capes Current and so be carried northwards; later in the year the flow would more likely be southward and so aid migration towards Rottnest Island.

The speed/time relationship in Figure 9 shows the time required to reach Rottnest Island from the Abrolhos Islands, Shark Bay and Ningaloo Reef at different mean current speeds. Using the typical current speeds summarised above and assuming direct southward transport, the larvae would probably travel at speeds of 5 to 15 cm/s (*i.e.*, < 15 km/day) and they would not reach Rottnest Island within the pelagic larval duration of about 3 weeks. In the Leeuwin Current, however, where mean southward speeds are likely to be at least 20 to 30 cm/s, Abrolhos-derived larvae could easily reach Rottnest, while at net speeds of 50 cm/s Shark Bay and perhaps even Ningaloo emerge as possible larval sources. Clearly, the observed variability in alongshore current speeds can greatly affect the likelihood of larval migration from the three possible sources up the west coast and hence the recruitment at Rottnest.

A more quantitative indication of the probability of passive larvae spawned at the Abrolhos Islands reaching the vicinity of Rottnest Island has been assessed using the web-based larval transport model Aus-Connie (Australian Connectivity Interface; Condie *et al.* 2005 – http://www.per.marine.csiro.au/aus-connie, verified February 2008). The model simulates larval trajectories from a specific source region using satellite-derived sea level data (and derived near-surface currents) with modelled wind fields over the period 1995 to 1999 to examine the connectivity between the source and sink regions. The output is the probability distribution of planktonic larvae in 0.5 degree latitude/longitude squares over an assumed larval lifetime (in our case, the 30-day option in the model is the most appropriate for *Abudefduf* larvae of those available).

Defining the source region as the 1-degree block 28.5° to 29°S, 113.5° to 114.5°E centred on the Abrolhos Islands, we summed the probabilities of all squares south of 31.5°S and within about 1 degree of Rottnest Island on the (perhaps naive) assumption that this would encompass all the larvae that have reached or passed within 100 km of the Island within the larval lifetime. We

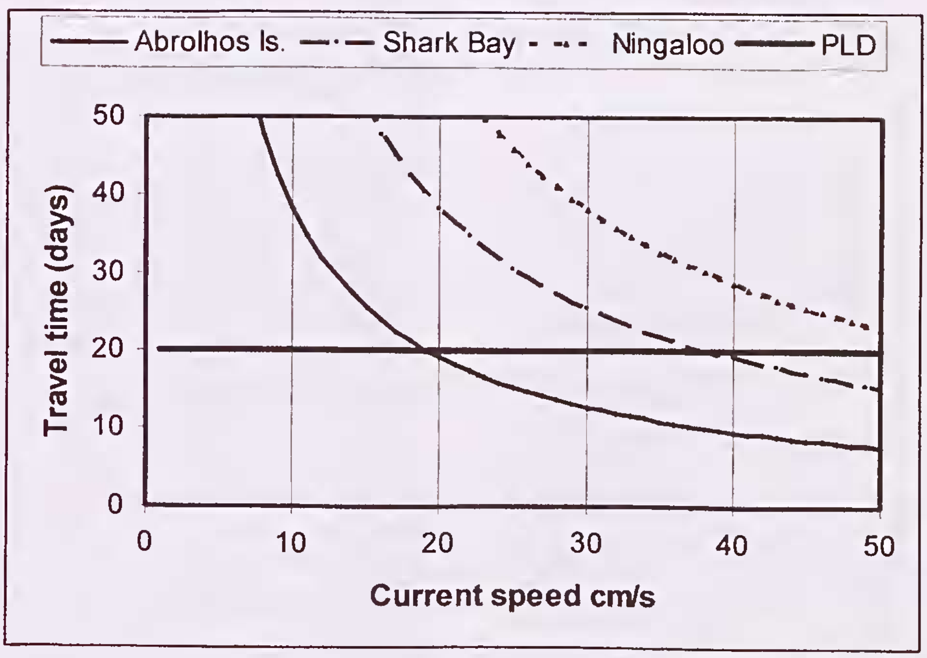

Figure 9. Speed/time relationship showing the time taken for planktonic larvae to reach Rottnest Island from the Abrolhos Islands (solid line), Shark Bay (dashed) and Ningaloo (dotted) at different mean current speeds. The pelagic larval duration of *Abudefduf* larvae has been set at 20 days (horizontal black line).

also noted the furthest southward travel of larvae in the 30-day period as an approximate indicator of the strength of the Leeuwin Current.

The results (not graphed here) clearly confirm that larvae could be carried well south of Rottnest Island by the Leeuwin Current – in some cases particles rounded Cape Leeuwin and were heading eastwards towards the Great Australian Bight within the month-long drift period. The results also indicate that larvae were widely dispersed offshore by the meander/eddy system and only a relatively small proportion of the original particles in fact passed anywhere near Rottnest Island. Adding to this the (unknown) larval mortality suggests that the likelihood of any particular larva dispersing from the Abrolhos Islands and recruiting at Rottnest is extremely small. Even though the Aus-Connie period 1995 to 1999 includes two of the peak recruitment years, the model did not reproduce the observed inter-annual abundances at Rottnest Island very well. This is almost certainly because of limitations of the simple processes incorporated into Aus-Connie (Condie *et al.* 2005) and also because of gaps in our knowledge of the biological attributes of the fish such as spawning strength, food availability and mortality.

Despite these limitations, modelling can provide a useful tool for comparing likely particle trajectories and hence the potential abundance of larval recruits at Rottnest Island over time. A finer resolution model with more flexible larval options (including swimming ability) is under development (Pearce *et al.* in prep.) and preliminary results confirm that larvae can be passively advected from the Abrolhos to Rottnest Island within 10 days (as suggested in Figure 9); many other larvae, however, will not arrive within their larval duration and so presumably perish. Even particles (larvae) released over successive 5-day intervals reveal a high level of variability in arrival times and abundance in the vicinity of Rottnest.

c) Cross-stream transport to the Island and local nearshore processes

Following their southward transport in the Leeuwin Current, the pelagic larvae are typically somewhere west of the continental shelf and need to reach the coastal waters of Rottnest Island by a combination of cross-shelf current/mixing processes, wind-driven surface currents (especially if the larvae are travelling under an algal raft), and active swimming. On finding suitable habitat, the larvae metamorphose to the juvenile stage and "settle" in the coastal reefs where they grow through the juvenile stage into adulthood, subject to suitable environmental conditions, adequate food, and predation.

Few current measurements have been made in the vicinity of Rottnest Island. Some early current observations (Cresswell *et al.* 1989) showed highly variable current patterns near Rottnest Island with occasional strong (20 to 30 cm/s) currents, while nearshore currents were generally much weaker: some measurements in Longreach Bay on the northern coast of the Island (Byrne 2001; Hopkin 2001) showed mean current speeds of < 5 cm/s with a peak of 17 cm/s. During each fish survey, the general flow of water in the vicinity of Pocillopora Reef was noted, showing that under typical southwesterly wind conditions warm offshore water flooded over the reef bringing in the new recruits, while with easterly winds cooler water from Porpoise Bay (to the northeast) displaced the warm water. It may be noted that, because of the micro-tidal range off the Perth coast, tidal currents in this area are negligible (Pearce *et al.* 2006a).

The wind regime off Rottnest Island in late summer (when the major *Abudefduf* recruitment tends to occur) is dominated by southerly winds modulated by the strong diurnal sea breezes (Masselink & Pattiaratchi 2001; Pearce *et al.* 2006a). These strong southerlies can result in an offshore near-surface Ekman transport of order 30 cm/s, overlying a weaker onshore current component (Muhling & Beckley 2007), so the vertical distribution of the larvae in the water column may govern whether they encounter onshore or offshore transport (Leis 2006), thus either assisting or hindering recruitment to the nearshore waters around Rottnest Island.

The wind would also directly affect drifting rafts of floating *Sargassum*, which can be packed with tiny fish (Hutchins 1995). These include both pre-settlement recruits as well as older larvae which have undergone metamorphosis and achieved full juvenile colouration under the raft. Some *Sargassum* rafts have been seen well west of Rottnest Island in the Leeuwin Current and can be quite extensive – on one occasion, a raft some 2 m wide and over a km long was seen 20 km west of Rottnest travelling south at 2 to 3 knots (BH). During the 1999 recruitment in particular, many large rafts of *Sargassum* washed into the bays along the south side of Rottnest and these were populated with small juveniles of tropical reef fish, including a number of category "b" *Abudefduf*'s. Over the years, many smaller patches of floating sargassum sampled near the south coast of Rottnest (Hutchins 1995) have in fact contained few or no *Abudefduf spp.*, so most of the *Abudefduf* recruits to Parker Point probably arrived as free swimming planktonic larvae.

There is little published information on the abundance, extent or seasonality of these algal rafts off the Western Australian coast. The possibility of marine larvae being transported down the coast under algal mats in the Leeuwin Current was suggested by Walker (1991), Dunlop (1997) and Dunlop & Rippey (1998) have reported Bridled Terns foraging over drift weed in coastal waters during late summer and early autumn. Fishers have also reported that such rafts or pontoons attract predatory fish (de Bruin 2007). The potential of drifting algal rafts to contribute to the dispersal of larval fish should be further investigated, both by direct observation/sampling and (for larger patches) using satellite remote sensing (Gower *et al.* 2006).

In addition to these oceanographic/meteorological processes which would passively transport planktonic larvae, late pre-settlement larvae are very competent swimmers. There is little direct information on the swimming capacity of our two *Abudefduf* species. Leis *et al.* (1996) directly observed the swimming behaviour of a number of coral reef larval fish (including one *A. sexfasciatus* and a second *A.* species), and suggested that "the faster fishes" were swimming at 20 to 30 cm/s, with the Pomacentrids being among the more competent swimmers. Experiments by Fisher *et al.* (2000) on *Pomacentrus amboinensis* confirmed that swimming ability increased with age/size, and was over 25 cm/s from an age of just 5 days after hatching. From an age of about 2 weeks, the larvae could swim 20 to 40 km over a period of up to 100 hours (*ibid.*). The growth rate and swimming endurance (and hence distance swum) of fish larvae can be greatly increased by active feeding during the swim (Leis & Clark 2005) so the food availability and type can be very important. While larval fish have been shown to swim directionally rather than at random (possibly following auditory and/or olfactory cues associated with the reef system – *e.g.*, Leis 2005), it is unclear whether they actively swim towards reef systems from some distance away or whether they passively encounter the reefs and then at close range seek out suitable settling habitat.

Based on the above, late stage *Abudefduf* larvae would have a likely swimming speed of about 10 to 20 cm/s, comparable with the ambient shelf currents which could therefore materially affect larvae either actively seeking or passively encountering the Island.

Water temperatures in February/March are at their summer peak of about 23 °C both offshore at Rottnest Island and near the coast at Marmion (Figure 1). These temperatures are maintained at Rottnest Island until about May (Figure 7b), before falling to about 19 °C in winter – these appear to be sufficient for the survival of newly-arrived *Abudefduf* larvae and juveniles, whereas any larvae near the coast would be unlikely to survive the nearshore winter temperatures of only 16 °C.

d) Inter-annual variability

The 2 major peaks in total *Abudefduf* abundance during the strong *La Nina* years 1999 and 2000 (Figure 5) were closely linked with the record high coastal sea levels and (larger-scale) surface temperatures in those years, and hence with an unusually strong Leeuwin Current (Figure 8). By contrast, the 1995 pulse in Figure 5 was at a time of relatively low sea level but this was also an anomalous year when the SST was high (Figure 8), suggesting that water temperature (rather than strong southward transport) may have contributed to the good recruitment that year by aiding rapid growth and survival. The lesser recruitment peak in 2001 (Figure 5) was during the fading stages of the 2000 *La Nina* when sea level was still elevated (Figure 8), but here the water temperature was marginally below average. Clearly, other (biological) factors also play an important role in recruitment, so successful recruitment requires both good larval supply and favourable environmental conditions.

Water temperature measurements in the continental shelf waters off south-western Australia have revealed a warming of about 1 °C over the past 5 decades (Pearce & Feng 2007). It is uncertain how this may directly affect recruitment at Rottnest Island, but there could well be a progressive southward range extension of tropical fish down the Western Australian coast. If water temperatures at Rottnest Island (present winter-to-summer range 19 to 23 °C – Figure 7b) were to approach those presently prevailing at the Abrolhos Islands (20 to 23.7 °C; Pearce 1997), it is possible that *Abudefduf* breeding populations could perhaps be sustained at the southerly location in the future.

Summary and Conclusions

Three decades of larval fish observations at Rottnest Island have shown the annual arrival of pulses of tropical fish larvae (two *Abudefduf* species have been examined here), most intensely in early autumn when water temperatures are still high and the Leeuwin Current is strengthening. The source of these larvae is almost certainly the Abrolhos Islands, and historical current measurements indicate that the Leeuwin Current is a more likely transport vector than the slower and more variable shelf currents. Recruitment is also possible from Shark Bay on occasion, and even (albeit rarely) Ningaloo Reef.

It is clear that both oceanographic and biological processes play very important roles in governing the seasonal and inter-annual levels of settlement. While we have shown that reasonable estimates of the ocean currents and their variability based on historical observations support the concept of southward inter-island transport, explaining the observed inter-annual fluctuations in settlement requires better knowledge of biological factors such as the larval abundance at the source (or spawning strength), and both mortality rates and food availability *en route*. Recent developments in hydrodynamic modelling of the current system are being undertaken to examine the dispersal/transport process in more detail, and the potential role of drifting rafts of *Sargassum* in the transport process also requires further investigation.

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